LYCOSID SPIDERS ON ARTIFICIAL FOLIAGE: STRATUM CHOICE, ORIENTATION PREFERENCES, AND PREY-WRAPPING[1]

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The majority of lycosid spiders neither spin webs for prey capture nor hunt actively, but spend most of their time waiting for prey at a resting site (Cragg, 1961; Edgar, 1969). In this regard, those lycosids that inhabit the herbaceous stratum resemble the aerial web-weaving spiders. As does a web, the foliage substratum provides a waiting site, a medium for transmission of vibratory stimuli produced by prey, and a surface on which capture is performed (Rovner and Knost, 1974). In the present study we used artificial foliage to examine stratum choice in *Lycosa punctulata* Hentz and *L. rabida* Walckenaer, which usually are found in the herbaceous stratum of fields, and in *Schizocosa saltatrix* (Hentz) and *S. crassipes* (Walckenaer), which typically are found on the leaf litter of forest floors. We also studied body orientation preferences shown by individuals of the first three species when they rested at an elevated site on the artificial foliage. The significance of a preference for vertical orientation was hypothesized with regards to equalizing proprioceptive input, minimizing energy expenditure, facilitating prey detection, and improving concealment from predators. Finally, we observed post-immobilization prey-wrapping to determine if this behavior is an adaptation for retention of captured prey by spiders dwelling in the herbaceous stratum, as hypothesized by Rovner and Knost (1974).

METHODS

Sokal and Rohlf (1969) was the source of all parametric statistical analyses. All means are accompanied by their standard deviation.

Spiders were collected in Athens Co., Ohio, USA, and main-tained under conditions described previously (Rovner and Knost, 1974). Adults of each species were examined during their natural season, i.e., when adults were abundant in the field. Studies were conducted in glass terraria ($0.2 \times 0.4 \times 0.2$ m high) contain-ing cardboard leaves with controlled surface areas and slopes. A 50-mm styrofoam layer on the bottom was covered with 5 mm of white sand, the latter being an inert substratum (Greenquist, 1975). Two cotton-stoppered vials provided drinking water. Cardboard plants, 0.18 m high and a mean width of 21 mm $\pm$ 6.0 (range $= 10$–30 mm), were inserted into the styrofoam so that the tops reached within 10 mm of the glass lid. Three foliage designs were used (Fig. 1):

Compound Design. This consisted of a vertical axis with one to four "leaf" projections coming off at 60° relative to the hori-zontal when viewed from an edge perspective. The surface area of the 60° slopes equaled the surface area of the vertical blades. There were nine to eleven "plants" per terrarium.

60° / 90° Simple Design. Individual vertical and 60° blades such that the surface area of the vertical slopes equaled that of the 60° slopes; ten vertical and nine 60° blades per terrarium.

60° Simple Design. All blades positioned at 60°; eleven or twelve blades per terrarium. When viewed from a surface rather than an edge perspective, all the blades (or leaves) of all three designs pointed directly upward.

The relative humidity in the terraria averaged 94% $\pm$ 3.8 and was maintained by a 250-ml bowl filled with cotton and distilled water. The high humidity minimized the possibility of a vertical gradient which otherwise might have influenced site selection, although Greenquist (1975) found that a difference of medium vs. high humidity levels ($< 65\%$ vs. $> 85\%$) had no effect on stratum preference in *L. punctulata*. Temperature within the terraria averaged 26.7° $\pm$ 4.5. The hygrometer and thermometer were housed in a terrarium identical to the test terraria but without foliage and spiders. Photoperiod was not controlled. Leaf litter was placed in the bottom of several terraria of the woodland-dwelling *S. saltatrix* to see if this influenced stratum preference.

Individual experiments were conducted from 9 to 14 days with one spider ("solo") or three individually marked spiders of the
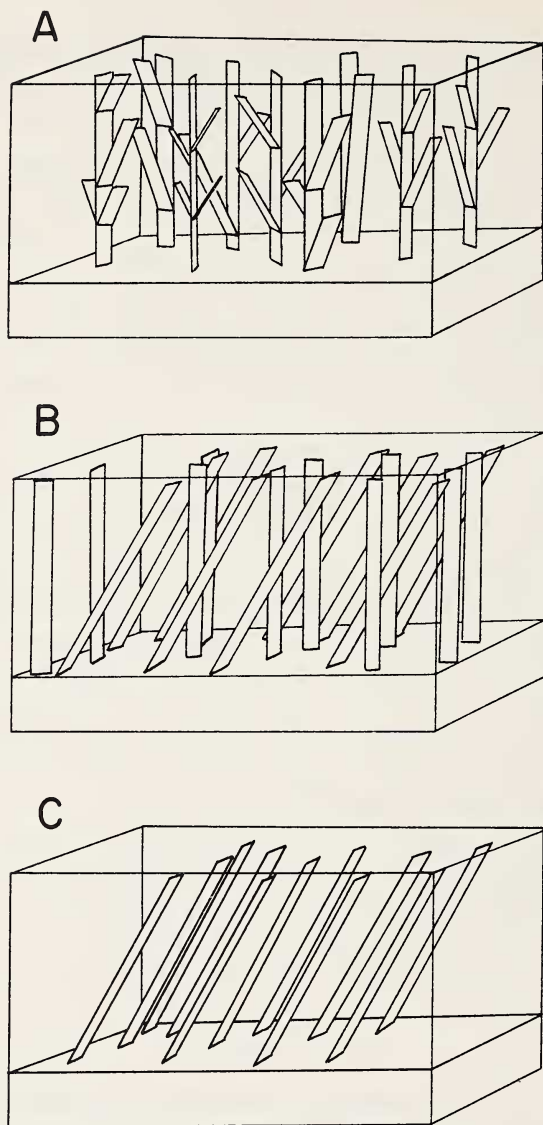
Fig. 1. Foliage designs used to study stratum choice and orientation preferences in lycosid spiders. (Water bowls and vials are not shown.) (A) Compound Design. (B) 60°/90° Simple Design. (C) 60° Simple Design.

same sex ("trio") in each terrarium. We observed the animals four times daily for 6 days at 3-hour intervals between 0900-1800. They were fed on the seventh day, and observations resumed on the eighth day. At each observation, the spider's height (from the center of the cephalothorax to the terrarium base), the slope of the resting site, and the orientation of the body relative to the blade or leaf axis were recorded. When cannibalism or death occurred (eleven cases) during trio experiments, replacement was made with equivalently marked animals. Five unmated females built egg sacs during the experiments; however, this did not influence stratum preference (paired-comparisons test with arcsine transformation; variation due to egg sac, $F_{s(1,4)} = 0.323$ NS; variation among individuals, $F_{s(4,4)} = 1.892$ NS).

RESULTS

Stratum choice. — The differences in time spent on foliage vs. on the ground were significant among the four lycosid species (one-way ANOVA with arcsine transformation; $F_{(3,56)} = 31.189$, $P < 0.001$). *L. punctulata* (12 females, 4 males) averaged 24.4% of the recorded position on the foliage (n = 832); *L. rabida* (5 females, 13 males) averaged 41.1% (n = 989); *S. crassipes* (3 females, 15 males) averaged 1.2% (n = 595); and *S. saltatrix* (13 females, 7 males) averaged 9.1% (n = 1022). An a posteriori STP-test revealed no significant difference in preference between the two *Lycosa* spp. *S. saltatrix* had significantly greater herbaceous preference than *S. crassipes* ($P < 0.05$) and significantly less than the *Lycosa* spp. ($P < 0.001$). *S. crassipes* is omitted from the following analyses due to its very low tendency to rest on the foliage.

Stratum choice by *L. punctulata* and *S. saltatrix* was not affected by variation in foliage design or animal density; however, the tendency to spend time on the foliage in *L. rabida,* while not affected by foliage design, was significantly greater at solo density (Table I). Data on the individuals of these three species are available in Greenquist (1975).

The presence of leaf litter in some of the terraria of *S.saltatrix* did not affect stratum preference for any foliage design (paired-comparisons test; Litter variation, $F_{s(1,2)} = 1.370$ NS; Foliage variation, $F_{s(2,2)} = 1.142$ NS). This suggested that these spiders (and probably *S. crassipes*) would not seek the artificial foliage when

Table I. Effect of spider density and foliage design on stratum choice in three lycosids. Individuals were grouped according to density and foliage design. An arcsine transformation was performed on the % of readings in which each spider was on the foliage. The mean % of each group was analyzed with two-way ANOVA without replication for solo vs. trio densities and for Compound vs. 60°/90° Simple vs. 60° Simple foliage designs.

Species	Source of variation	df	Mean square	F_s
	Density	1	94.72	1.52 NS
Lycosa punctulata	Foliage design	2	19.50	0.31 NS
	Error	2	62.27	
	Density	1	570.38	48.76*
Lycosa rabida	Foliage design	2	23.62	2.02 NS
	Error	2	11.70	
	Density	1	0.001	0.00 NS
Schizocosa saltatrix	Foliage design	2	7.07	0.15 NS
	Error	2	46.03	

*$P < 0.05$

the leaf litter, characteristic of their natural habitat, was not available in the experimental terraria.

Orientation preferences. — Leaf slope preference was analyzed by chi-square; we assumed that random preference would result in an equal number of positions recorded on vertical and 60° slopes. *L. punctulata* had a significant preference for the 60° slope over the vertical slope on the compound foliage design; *L. rabida* and *S. saltatrix* showed no preference on this foliage design (Table II). *L. punctulata* was found on the vertical slope more often than on the 60° slope when housed with the 60°/90° Simple Design. *L. rabida* and *S. saltatrix* preferred the 60° slope in this case.

We assumed that random selection of upper vs. lower surfaces on the 60° slopes would result in an equal number of positions recorded for each surface. Chi-square analysis indicated that all three species showed a significant preference for the upper surface on all three foliage designs (Table II).

The orientation of the spider within the plane parallel to the surface on which it rested was recorded as the angular difference between the blade (or leaf) axis and the spider's body axis. This

Table II. Total numbers of resting sites recorded in three lycosid species on different surfaces of three foliage designs. Chi-square (df = 1) values for (a) 60° slope vs. vertical and (b) upper vs. lower surfaces of 60° slopes are given.

	Compound Design			60°/90° Simple Design			60° Simple Design	
	60°		Vertical	60°		Vertical		
	Upper	Lower		Upper	Lower		Upper	Lower
Lycosa punctulata	28	1	11	16	0	34	102	7
(a)	25.138***			16.000***				
(b)		8.100**			6.480*		82.798***	
Lycosa rabida	70	9	80	59	3	42	124	19
(a)	47.101***			50.581***				
(b)		0.006 NS			3.846*		77.098***	
Schizocosa saltatrix	14	1	14	19	0	7	32	4
(a)	11.267***			19.000***				
(b)		0.034 NS			5.538*		21.778***	

*P < 0.05
**P < 0.01
***P < 0.001

was measured clockwise to the nearest 30° interval, with 0° = facing directly upward (Fig. 2). Two-way ANOVA was used to determine angular preferences within species and differences among species. There was a significant difference in preference within species ($F_{s(11,22)}$ = 13.943, $P < 0.001$), indicating that individuals had a preferred orientation on the artificial leaf. There was no difference, however, in angular preference among species ($F_{s(2,22)}$ = 0.752 NS). Orientation to 180° (= facing directly downward) was significantly greater for the three species than to all other angles (a posteriori STP-test, $P < 0.001$). Orientation to 0° (directly upward) was significantly greater than to all other angles except 180° ($P < 0.01$). Orientation to 180° was significantly greater than to 0° ($P < 0.05$). Spiders were not found to orient differently on the 60° and vertical slopes (paired-comparisons test; *L. punctulata*, $F_{s(1,11)}$ = 2.560 NS; *L. rabida*, $F_{s(1,11)}$ = 1.016 NS; *S. saltatrix*, $F_{s(1,11)}$ = 1.194 NS).
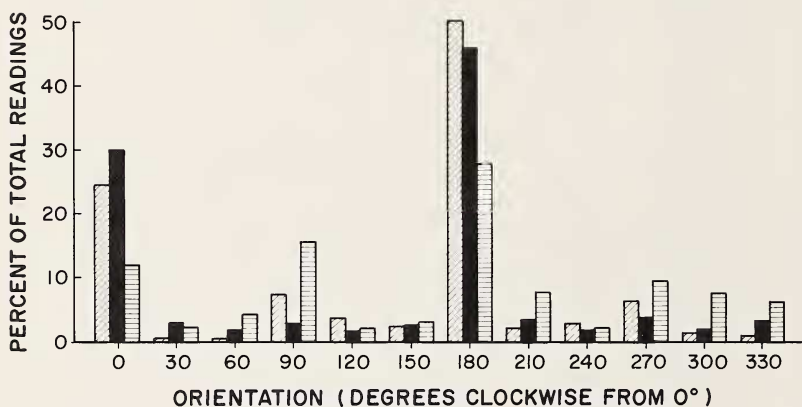

Fig. 2. Body orientation when resting on artificial foliage in *Lycosa punctulata* (obliquely hatched bar) (n = 203), *L. rabida* (solid bar) (n = 399), and *Schizocosa saltatrix* (horizontally hatched bar) (n = 93). 0° = facing directly upward.

Since the predominant orientation in the three species was vertical (0° and 180°), there was the possibility of the data being biased due to the spider's grasping the edges of the vertically positioned leaves with its right or left tarsal claws. Therefore, we conducted additional experiments in four other terraria, using female *L. rabida*. Each of these terraria was subdivided into five,

equal-size compartments by parallel cardboard sheets placed ver-
tically (two terraria) or at an oblique (60°) angle (two terraria).
These sheets extended the full width and height of the terraria,
and were held in place by strips of masking tape along the side
and bottom edges. Thus, each of the twenty spiders lived in a
compartment with a narrow horizontal floor, two tall broad card-
board walls, and narrow glass sides and top. (These lycosids can-
not climb glass.) Observations were made on 11 days, four times
per day, as above.

Under these conditions, the spiders were recorded on the card-
board walls in 91.9% of the 834 total positions recorded; i.e., they
usually were at an elevated location. In the oblique wall condi-
tion, 95.5% of the 448 positions were on the wall providing an
upper surface; i.e., the spider rarely adopted a position on the
undersurface of the overhanging wall.

Of the 750 positions recorded on walls, under both vertical and
oblique wall conditions, 21.7% were noted in which the spider
held onto the top edge (the only available edge) of the cardboard.
Most of these (69.3%) involved a 90° or 270° body orientation,
since the edge-holding spider typically used the tarsal claws of
the four legs of the right or left side to secure the hold.

Most (78.3%) of the wall positions adopted were on the broad
surface. Here, in the absence of an edge cue, 43.4% of the posi-
tions were 0° (22.3%) or 180° (21.1%), i.e., facing directly up or
down. The next most common orientation on the broad surface
(18.6%) was with the body parallel to the ground, i.e., at 90° or
270°. No significant differences between the orientation prefer-
ences of the spiders on these broad surfaces and the spiders on
the artificial foliage were found (paired-comparisons test with
arcsine transformation; $F_{s(1,11)} = 1.014$ NS).

Prey-Wrapping

Methods. — Prey-wrapping behavior was examined in the
artificial foliage terraria after prey were withheld from the spiders
for up to 8 days. Prey items that either singly or in multiples of
three or four would approximate the size of the spider's body were
chosen to maximize prey-wrapping in the *Lycosa* spp. (Rovner
and Knost, 1974). *L. punctulata* were given crickets (*Gryllus* sp.
and Nemobiinae); *L. rabida* were fed grasshoppers (Cyrtacantha-
cridinae). On several occasions, when prey-wrapping occurred

on the foliage, the spider was chased from the prey with a soft brush to determine if the prey item was attached to the substrate and if the spider returned to the prey. *S. crassipes* and *S. saltatrix* were fed plant bugs (Miridae), thirty to forty bugs being placed in each terrarium. Multiple captures of up to six prey occurred, which should have stimulated prey-wrapping (ibid.).

Sod (with vegetation intact) from the habitat of *L. rabida* was placed in a 0.5 × 0.26 × 0.3 m high glass terrarium and brought into the laboratory. After prey were captured in the home cage of an individual of this species, the spider was coaxed onto the grass of the terrarium, where it came to rest, still holding its prey. Observation periods for prey-wrapping studies lasted 2 hr.

Results. — Prey transport was common in all four species and usually occurred before the prey were immobile. Immobile prey occasionally were transported from the ground into the foliage by all species except *S. crassipes*. Spiders transported prey with the chelicerae and walked with the body raised up; nevertheless, large prey often dragged on the ground.

None of the species used silk to immobilize the prey. In the two *Lycosa* spp., females exhibited from one to five separate bouts (and males only one bout) of post-immobilization wrapping during the 2-hr observation period in response to single large prey and multiple captures of small prey. While *L. punctulata* wrapped in a counter-clockwise direction, *L. rabida* wrapped 65.3% of the time in a clockwise direction. *L. rabida* held prey in the chelicerae during the first wrapping bout for an average of 1.6 ± 1.21 revolutions. Consequently, as the spider wrapped, the prey beneath it pivoted around with the spider. The spider then released the prey and continued to pivot above it for the rest of the bout. Holding the prey in this manner while wrapping rarely occurred during subsequent bouts, only appearing if those bouts were preceded by excessive prey manipulation with the palps, and never lasted as long as it had in the original bout. *L. punctulata* never held prey in this manner while wrapping. Other details of wrapping resembled the description of Rovner and Knost (1974) and are provided in Greenquist (1975). Wrapping never occurred in *S. crassipes* (four females, nine males) nor *S. saltatrix* (fifteen females, nine males).

L. rabida was examined under the semi-natural conditions of a terrarium containing field sod. Here, with the spiders holding

onto blades of tall grass, prey-wrapping was slower than it had been on the broader, flat surfaces of the artificial foliage terraria (one-tailed *t*-test; $t_{(46)} = 2.922$, $P < 0.01$). When the spiders were driven 90 mm or more from the feeding site (with a soft brush), they returned after as much as 2.5 min later in four out of six cases, and resumed feeding on the prey package still attached to the grass. On two occasions they came back by a different route than the one by which they had left. On another occasion a spider carried wrapped prey for 33 mm, dropped it (when touched by the brush), and continued on for another 85 mm. After 72 sec the spider returned to the drop site, although it id not find the prey, which had fallen to a point 30 mm below.

DISCUSSION

Stratum choice. — The selective advantage for any species to carry on a major portion of its activity in a specific micro-habitat is that this prevents interspecific competition. Kuenzler (1958) found that vertical stratification separates *L. rabida* from the ground-dwelling lycosids. The same would be true later in the year when *L. punctulata* replaces *L. rabida* in the herbaceous stratum. The results of our laboratory study support the idea of differential use of two strata by lycosids. The herbaceous stratum-dwelling *Lycosa* spp. spend significantly more time resting on the artificial foliage than the two *Schizocosa* spp., which are found in nature on woodland floors.

While overall habitat selection was found to depend on the ability of various lycosid species to withstand desiccation (Cherrett, 1964), the importance of the physical form of features within a lycosid's habitat in determining their micro-habitat distribution was emphasized by the field studies of Duffey (1962, 1966) and the work of Richter (1970). We found that our lycosids spend dissimilar amounts of time, depending on species, in different strata under conditions of uniformly high relative humidity and minimal (if any) temperature and light gradients. Thus, our data provide laboratory support for the idea that a preference for structural features within the habitat can play an important role in the micro-habitat distribution of wandering spiders.

In our experimental terraria (Fig. 1) foliage design had no effect on stratum choice (Table I). Density (solo vs. trio) had an effect only in *L. rabida,* the reason for which we do not know. (Unlike

L. punctulata, most of our *L. rabida* were males, which may tend to wander more and to interact agonistically at trio density, thereby spending less time resting at an elevated foliage site. This is only a guess.)

Orientation preferences. — Leaf slope preferences on the artificial foliage were not consistent among and even within the species, some spiders being located most often on a 60° slope, others most often on a vertical surface (Table II). These data, as well as the readiness of control spiders to rest on both 60° and vertical broad surfaces, suggest that there possibly is no preference for oblique vs. vertical leaves as resting sites in these lycosids.

There was a definite preference, however, for upper- rather than undersurfaces of sloping (60°) leaves (Table II). Similarly, control spiders on the broad surfaces rarely rested while holding onto the undersurface of a 60° cardboard wall. An inverted position likely provides less secure "footholds" for resting or for chasing prey in these webless spiders. It also is less suitable for the critical act of pouncing on the prey. since the spider would have gravity working against it.

Most aerial web-weaving spiders orient in a face-down position while resting in their webs (Eberhard, 1967). Orientation preferences also were shown by our lycosids on sloping or vertical surfaces, the spider most often adopting a vertical position. As with web weavers, a vertical position possibly yields optimum "clawholds" with the least amount of energy expenditure while waiting for prey. On artificial foliage, the most common resting position for lycosids, like that of web weavers, was facing directly downward. On a broad surface, the vertical orientation was again predominant, although the lycosids here faced up as often as down. Either way, equivalent input from the proprioceptors of the right and left sides is achieved, which may be the primary determinant of this orientation.

Visual and mechanical prey-detection by wandering spiders resting in the herbaceous stratum probably are enhanced by vertical orientation on stems or grass blades, since this aims the spider in one of the two main directions from which crawling prey are most likely to approach. Kuenzler (1958) noted that crawling prey are the primary food of lycosids.

A preferred vertical orientation on grasses and other plants may have influenced selection for the bold stripes running length-

wise on the two *Lycosa* spp. found in this stratum, since such markings would provide cryptic coloration. Ground-dwelling lycosids lack such bold, anterior to posterior, striped patterns.

The next most common orientation on artificial foliage and on broad surfaces was perpendicular to the vertical one, i.e., 90° or 270° (when 0° = facing up). In such a horizontal position on a sloping or vertical surface, the spiders were holding primarily by the tarsal claws of the upper four ipsilateral legs. For some reason, positions intermediate between vertical and horizontal are less satisfactory for long-term resting postures on elevated surfaces. It may relate to the effective use of the inwardly curving tarsal claws for securing a grip or to a tendency to prefer similar proprioceptive inputs from four ipsilateral legs as the next best condition to that provided by the bilaterally symmetrical input of a vertical orientation. All things considered, it is likely that vertical orientation would predominate in the field, where stems and the edges of grass blades provide largely vertical grasping sites for the claws that would add to the laboratory-demonstrated preference for a vertical position.

Prey-wrapping. — Our data supported Rovner and Knost's (1974) hypothesis that post-immobilization wrapping of prey by wandering spiders is an adaptation for successful feeding in the herbaceous stratum. This behavior did not occur in our ground-dwelling *Schizocosa* spp. Wrapping prevents prey loss from elevated sites when the cheliceral grip is relaxed during feeding, grooming, or a startle response, since wrapping always includes attachment of the prey to the site. Furthermore, when we forced spiders to leave immobilized prey, they were able to return to the site. Obviously, wrapped (i.e., attached) prey are far more likely to be recovered at an elevated site than are non-wrapped. Since the spiders sometimes returned by a route different from that taken when chased away, they were not depending on draglines to relocate the prey. They may have used kinesthetic orientation, or visual orientation, or both (Görner, 1966).

Rovner and Knost (1974) also suggested that wrapping by lycosids might serve to free the spider for subsequent attacks on additional prey, as occurs in web weavers. Out data did not support this idea. Subsequent captures were never observed in which the spider returned to the original prey at a previous site, as was also noted to be the case in *Cupiennius salei* (Melchers, 1963). Ap-

parently, in contrast to web-dwellers, which are likely to detect a prey while still handling a previous one (Eberhard, 1967) and which spend prolonged periods at fixed sites (in their webs), the retention of prey at a site for future use after additional captures is of little value to a wandering spider.

Summary

When housed in terraria, *Lycosa punctulata* and *L. rabida* spend significantly more time on artificial foliage than do *Schizocosa crassipes* and *S. saltatrix*. Such data provide laboratory support for the idea that a preference for structural features within the habitat plays a role in the micro-habitat distribution of wandering spiders. Our lycosid species prefer upper rather than lower surfaces as rest sites. and we suggest that upper surfaces are coincidentally more suitable for prey capture. On broad, steep surfaces our species most often adopt a vertical orientation, facing directly up or down. On artificial foliage, vertical orientation likewise predominates, with a significant preference here for a face-down position, i.e., the position also typical of web-weaving spiders. We suggest mechanisms, one of which may underlie this orientation preference. Coincidentally, prey detection by wandering spiders that are at rest in the herbaceous stratum may be facilitated by a vertical orientation. Our observations on post-immobilization prey-wrapping indicate that wrapping not only enables wandering spiders to retain prey while feeding at an elevated site, but also insures the recovery of immobilized prey when the spider momentarily flees and then returns to the feeding site.

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